

TAXONOMIC NOTES ON *LAURENCIA PARVIPAPILLATA* (CERAMIALES, RHODOPHYTA) FROM THE WESTERN PACIFIC

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ABSTRACT — The red alga *Laurencia parvipapillata* Tseng (Rhodomelaceae, Ceramiales) is characterised by the following set of features: 1) decumbent or prostrate thalli with conspicuously dorsiventral organisation; 2) distichous branching; 3) the production of two periaxial cells from each vegetative axial segment; 4) the sporadic occurrence of longitudinally and laterally oriented secondary pit-connections between contiguous superficial cortical cells; 5) the presence of projecting superficial cortical cells; 6) the presence of a palisade-like cortical layer; 7) the absence of lenticular thickenings in the walls of medullary cells; 8) the absence of *corps en cerise*; 9) a perpendicular arrangement of tetrasporangia; 10) the production of three tetrasporangium-bearing (an ordinary and two additional, the second to fourth) periaxial cells per fertile segment of tetrasporangial branches; and 11) spermatangia with distally-positioned nuclei.

RÉSUMÉ — L'algue rouge *Laurencia parvipapillata* Tseng (Rhodomelaceae, Ceramiales) est caractérisée par l'ensemble des éléments suivants : 1) des thalles prostrés ou décombants avec une organisation dorsiventrals caractéristique ; 2) une ramification distique ; 3) la production de deux cellules périaxiales par chaque segment axial végétatif ; 4) la présence sporadique de synapses secondaires orientées longitudinalement et transversalement entre les cellules corticales superficielles ; 5) la présence de cellules corticales superficielles saillantes ; 6) la présence d'une assise corticale palissadique ; 7) l'absence d'épaississements lenticulaires dans les parois des cellules médullaires ; 8) l'absence de corps en cerise ; 9) une disposition, perpendiculaire à l'axe des rameaux, des tétrasporocystes ; 10) la production de trois cellules périaxiales portant des tétrasporocystes (une normale, la deuxième, et deux additionnelles, les troisième et quatrième) par segment fertile des rameaux carpogoniaux ; et 11) des spermatocystes dans lesquels les noyaux sont positionnés distalement. (Traduit par la Rédaction).

KEY WORDS: Ceramiales, *Laurencia parvipapillata*, marine algae, Pacific, Rhodomelaceae, Rhodophyta, Taxonomy.

INTRODUCTION

The red alga *Laurencia parvipapillata* Tseng (Rhodomelaceae, Ceramiales) was described on the basis of material collected at Hong Kong by Tseng (1943) and has been widely reported from the Indo-Pacific (Dawson, 1954; Saito, 1969; Cribb, 1983; McDermid, 1988b; Nam, 1990; Silva *et al.*, 1996). Saito (1969) placed this species in the subgenus *Chondrophyucus*, which was followed by Zhang & Xia (1985). However, the occurrence of longitudinally oriented secondary pit-connections between contiguous superficial cortical cells (Cribb, 1983; Nam, 1990) and a perpendicular arrangement of its tetrasporangia (Tseng 1943, Zhang & Xia 1985; Nam, 1990) require a reconsideration of its subgeneric position (McDermid, 1989; Nam & Saito, 1995). In this paper we present some morphological features of *L. parvipapillata* collected from Japan, Vietnam and Malaysia and confirm its subgeneric status.

MATERIALS AND METHODS

Specimens examined were collected at the following localities, and voucher specimens are deposited in the Herbarium of Graduate School of Science, Hokkaido University, Sapporo (SAP 062657-062666) and in the Herbarium of College of Science, University of the Ryukyus, Nishihara (RYU). Japan: Oohara, Gushikawa-son, Kumejima Island, the Ryukyu Islands, 25.iii.1997 (vegetative, tetrasporangial and spermatangial), *leg.* S. Kamura, M. Masuda & T. Abe; Sesoko, Motobu-cho, Okinawa Island, the Ryukyu Islands, 30.iii.1991 (vegetative, tetrasporangial and spermatangial), *leg.* M. Baba; Bisezaki, Motobu-cho, Okinawa Island, 13.v.1991 (vegetative, tetrasporangial and spermatangial), *leg.* S. Kamura & M. Masuda, 20.iii.1992 (vegetative and tetrasporangial), *leg.* S. Kamura & M. Masuda. Vietnam: Con. Nha Trang, Khanh Hoa Province, 5.iii.1992 (vegetative), *leg.* M. Masuda; Hon Tre Island, Tien Hai Islands, Hatien, Kien Giang Province, 7.ii.1993 (spermatangial and tetrasporangial), *leg.* M. Masuda. Malaysia: Pulau Manukan, Kota Kinabalu, Sabah, 1.i.1996 (tetrasporangial), *leg.* M. Masuda. For most purposes, specimens fixed and preserved in 10% formalin/seawater were used, but living specimens from Kumejima Island and Okinawa Island were transported live to Hokkaido University, Sapporo, to confirm the presence/absence of spherical cell inclusions (*corps en cerise*). Sections were made by hand using a razor blade and pith stick. The sections of fixed materials were mounted in 50% glycerol/seawater on microscope slides and stained with 0.5% (w/v) cotton blue in a lactic acid/phenol/glycerol/water (1:1:1:1) solution. Those of living material were immediately mounted in seawater on microscope slides.

Position of spermatangial nuclei was examined according to the following procedure. Branches bearing male trichoblasts were excised from a formalin/seawater-preserved specimen (Kumejima Island, 25.iii.1997) and washed in tap water for 30 min. Detached spermatangial branches were pipetted onto microscope slides and stained with a $1 \mu\text{g ml}^{-1}$ solution of DAPI (4',6-diamidino-2-phenylindole) for 30 min. Fluorescence of nuclear DNA stained with DAPI was observed using a Nikon epifluorescence microscope X2F-EFD2 equipped with a mercury fluorescence lamp (Osram HBO 100 W/2) and a filter cassette UV-2A (EX330-380, DM400, BA420).

OBSERVATIONS

Plants grow on dead coral (Japan), limestone (Vietnam) or epiphytically on *Laurencia tropica* Yamada (Malaysia) in the lower intertidal zone on reef flats. Plants are 14-35 mm long, dark red to brownish red, cartilaginous, and adhere imperfectly to paper upon drying. One to four main axes (Fig. 1) develop from a small discoid holdfast 1.8-3.5 mm in diameter. The main axis are decumbent or prostrate and often bear secondary discoid holdfasts on the ventral surface which attach to the substratum. They are terete just above the basal disc and 0.8-1.0 mm in diameter, becoming abruptly compressed and 1.6-2.0 mm wide at the middle to upper (Fig. 2) portions. First-order branches are distichously formed along the main axis (Fig. 1). The majority of these branches are less than 1 mm long, whereas only several of them grow to 2-15 mm long and form further branches of up to four orders. Reproductive structures are produced by ultimate and penultimate branches. Secondary discoid holdfasts sometimes unite contiguous branches. Adventitious branches are sometimes formed in the lowest portions of the main axes.

The growing point is always sunk in an apical pit, as is typical of the genus. Each axial cell produces two periaxial cells (Fig. 3A-C). Superficial cortical cells are elliptical to rounded polygonal in surface view and irregularly arranged in longitudinal rows (Fig. 4). Superficial cortical cells on the dorsal side are 6-18 μm long by 6-12 μm wide (a length:width ratio of 0.6-1.8) in surface view in the distal portions of first-order branches, 13-22 μm long by 4-9 μm wide (a length:width ratio of 1.7-3.9) in the middle portions, and 6-17 μm long by 6-20 μm wide (a length:width ratio of 0.6-1.7) in the proximal portions. Superficial cortical cells on the ventral side are 6-18 μm long by 15-28 μm wide (a length:width ratio of 0.3-0.9) in surface view in the distal portions of first-order branches, 6-18 μm long by 12-25 μm wide (a length:width ratio of 0.4-0.9) in the middle portions, and 5-12 μm long by 12-24 μm wide (a length:width ratio of 0.3-0.7) in the proximal portions.

Superficial cortical cells are radially elongated and form a palisade-like layer (Figs 5, 6): the cells on the dorsal side (Fig. 5) are more conspicuously elongated than those on the ventral side (Fig. 6). Superficial cortical cells of the ventral side are more deeply pigmented than those of the dorsal side. The superficial cortical cells of the dorsal side in transverse sections are 22-42 μm thick (a thickness:width ratio of 2.2-5.3), in the distal portions of first-order branches, 25-42 μm thick (a thickness:width ratio of 2.8-6.6) in the middle portions and 24-38 μm thick (a thickness:width ratio of 1.9-5.0) in the proximal portions. Those of the ventral side are 20-40 μm thick (a thickness:width ratio of 1.1-2.5), in the distal portions of the first-order branches, 18-40 μm thick (a thickness:width ratio of 1.1-3.1) in the middle portions and 27-44 μm thick (a thickness:width ratio of 1.2-4.6) in the proximal portions. The superficial cortical cells project conspicuously at the middle to upper (Figs 5, 6) portions of the thallus. Longitudinally oriented secondary pit-connections are sporadically present between contiguous superficial cortical cells (Fig. 7). Laterally oriented secondary pit-connections (Fig. 8) and lateral fusions (Fig. 9) are also sporadically present between contiguous superficial cortical cells. Superficial cortical and trichoblast cells do not contain *corps en cerise* (Figs 4, 10). Medullary cells have no lenticular thickenings on the walls. Medullary cells are 80-160 μm in diameter in the middle to lower portions of the first-order branches and have walls of 5-10 μm in thickness. Cortical and medullary cells are closely packed, and intercellular spaces are absent between the cells.

Tetrasporangia are formed on distal portions (Fig. 11) of the first- to fourth-order branches that are 500-900 μm long and 600-800 μm wide. The tetrasporangium initial is cut off from an elongated periaxial cell towards the abaxial side (Figs 12, 13). Three periaxial cells in each fertile segment conspicuously elongate towards the thallus surface (Fig. 14) and produce tetrasporangia; one (the first) periaxial cell remains vegetative. Thus, two fertile (the third and fourth) periaxial cells are additionally produced. Each tetrasporangium is provided with two cover cells which are distally produced by the fertile periaxial cell (Figs 12, 13, 15). Tetrasporangia become mature centripetally and show a perpendicular arrangement relative to the longitudinal axis of the bearing branch almost until maturity (Fig. 11). Mature tetrasporangia with tetrahedrally arranged spores (Fig. 15) are 100-120 μm long by 60-80 μm wide.

Male trichoblasts are formed in cup-shaped pits of first- to fourth-order branches that are 600-1000 μm long by 600-900 μm wide (Fig. 16). Spermatangial branches arise from the suprabasal segment of the trichoblasts (Fig. 17) and terminate in single, large, obovoid to spherical sterile cells 20-30 μm in diameter (Fig. 18). Spermatangia are ellipsoidal, 8-10 μm long by 4-6 μm wide, and their distal portions are deeply stained with cotton blue (Fig. 18). Nuclei are distally placed when visualised following DAPI staining (Fig. 19). Cystocarpic plants were not collected.

DISCUSSION

Laurencia includes two subgenera, *Laurencia* and *Chondrophyucus* Tokida *et* Saito (Saito, 1967). The subgenus *Laurencia* was characterised by the presence of longitudinally oriented secondary pit-connections between contiguous superficial cortical cells and a parallel arrangement of tetrasporangia, whereas the *Chondrophyucus* was characterised by the absence of such pit-connections and a perpendicular arrangement of tetrasporangia (Saito, 1967). However, species with a mixture of these subgeneric features have been found by more recent studies (Wynne & Ballantine, 1991; Nam & Saito, 1991b; Ballantine & Aponte, 1995; Nam & Sohn, 1994; Fujii & Cordeiro-Marino, 1996; Fujii *et al.*, 1996) and obscure the difference between the subgenera. According to Nam & Saito (1995), however, the two subgenera are clearly distinguished by the number of periaxial cells produced from each vegetative axial segment: four in *Laurencia* and two in *Chondrophyucus*. The production of two periaxial cells from each vegetative axial segment in *L. parvipapillata* confirms its subgeneric position as *Chondrophyucus*.

Nam (1990) reported cell inclusions, which were contained in his Hawaiian material of *L. parvipapillata* preserved in formalin/seawater for about 20 years, as vestiges of *corps en cerise*. However, McDermid (1988b) reported the absence of *corps en cerise* in *L. parvipapillata* from the Hawaiian Islands, which was confirmed in our living material from the Ryukyu Islands nearer to the type locality, Hong Kong (Tseng, 1943). *Corps en cerise* often become damaged during examination of living material under microscope (unpublished observations). Cell inclusions like *corps en cerise* can be found in specimens of some species which were preserved in formalin/seawater for a short period (within a few days), but the inclusions disappear soon (unpublished observations). Thus, *corps en cerise* are ephemeral in fixed material (Maggs & Hommersand, 1993). The identity of Nam's (1990) vestiges of *corps en cerise* is uncertain. *Corps en cerise* have not been found in species of *Chondrophyucus* (McDermid, 1988b; Fujii *et al.*, 1996; Masuda *et al.*, 1997a,

1998, and unpublished observations), but are contained in species of the subgenus *Laurencia* (McDermid 1988a; Masuda *et al.*, 1996, 1997a). The presence or absence of *corps en cerise* may be a further critical feature used to distinguish between the subgenera *Laurencia* and *Chondrophyucus*. However, reports of the presence/absence of *corps en cerise* have been limited for relatively few species.

Laurencia parvipapillata was named on the basis of presence of conspicuously projecting superficial cortical cells (Tseng, 1943). Of species with such cells, the following species can be included in the subgenus *Chondrophyucus*: *L. carolinensis* Saito (1969), *L. cartilaginea* Yamada (Nam & Saito, 1990), *L. dotyi* Saito (1969), *L. gemmifera* Harvey (Fujii *et al.*, 1996) and *L. iridescens* Wynne *et* Ballantine (1991). These species all differ from *L. parvipapillata* by the absence of a palisade-like cortical layer (Saito, 1969; Nam & Saito, 1990; Wynne & Ballantine, 1991; Fujii *et al.*, 1996).

Laurencia parvipapillata is further characterised by the conspicuous dorsiventrality and different dimensions of superficial cortical cells between the dorsal and ventral sides. Although the latter situation has not been reported in other species of this genus, we predict that it will be found in species having decumbent or prostrate thalli, especially those having compressed to flattened axes.

Species of the subgenus *Chondrophyucus* usually produce additional tetrasporangium-bearing periaxial cells (Nam & Saito, 1995; Fujii & Cordeiro-Marino, 1996; Fujii *et al.*, 1996; Masuda *et al.*, 1998). On the other hand, species of the subgenus *Laurencia* which are characterised by the production of four periaxial cells from each vegetative axial segment do not bear additional tetrasporangium-bearing periaxial cells (Nam & Saito, 1995; Masuda *et al.*, 1996, 1997b). *Laurencia maris-rubri* Nam *et* Saito (1995) in the subgenus *Chondrophyucus* do not produce additional tetrasporangium-bearing periaxial cells. Thus, the number of tetrasporangium-bearing periaxial cells in *Chondrophyucus* is diverse and is a good taxonomic feature at the species level (Nam & Saito, 1995; Fujii & Cordeiro-Marino, 1996; Fujii *et al.*, 1996; Masuda *et al.*, 1998). According to Nam & Saito (1995), the species that share the character of the second periaxial cell forming the tetrasporangium may belong to a monophyletic assemblage. These are *L. capituliformis* Yamada (Nam & Saito, 1995), *L. gemmifera* (Fujii *et al.*, 1996), *L. intermedia* Yamada (Nam & Saito, 1995), *L. iridescens* (Nam & Saito, 1995), *L. maris-rubri* (Nam & Saito, 1995), *L. palisada* Yamada (Masuda *et al.*, 1998), *L. papillosa* (C. Agardh) Greville (Nam & Saito, 1991a), *L. parvipapillata* (Nam & Saito, 1995; present paper), *L. poiteaui* (Lamouroux) Howe (Fujii *et al.*, 1996) and *L. tumida* Saito *et* Womersley (Nam & Saito, 1995). However, the number of periaxial cells in the procarp-bearing segment of female trichoblasts is not uniform in these species: four in *L. capituliformis* (Nam & Saito, 1995), *L. intermedia* Yamada (Nam & Saito, 1995), *L. palisada* (Masuda *et al.*, 1998) and *L. tumida* (Nam & Saito, 1995) and five in *L. gemmifera* (Fujii *et al.*, 1996) and *L. poiteaui* (Fujii *et al.*, 1996) so far as known. Furthermore, some of the ten species have a palisade-like cortical layer (*L. capituliformis*, *L. intermedia*, *L. palisada*, *L. papillosa*, *L. parvipapillata* and *L. tumida*), while others do not. At present it is difficult to conclude that the last-mentioned tetrasporangial and procarpic features have phylogenetic significance in the genus *Laurencia* as stated by Nam & Saito (1995).

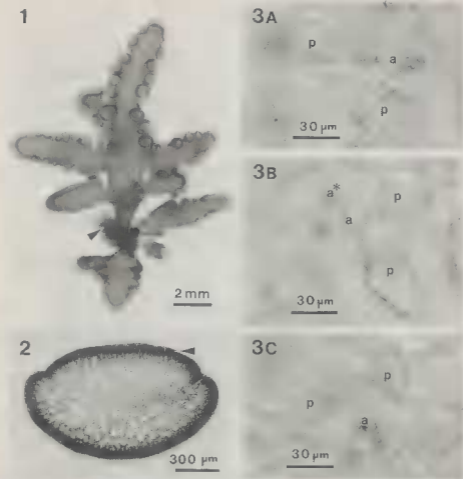
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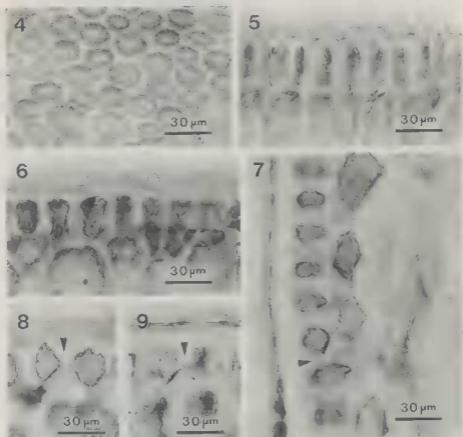
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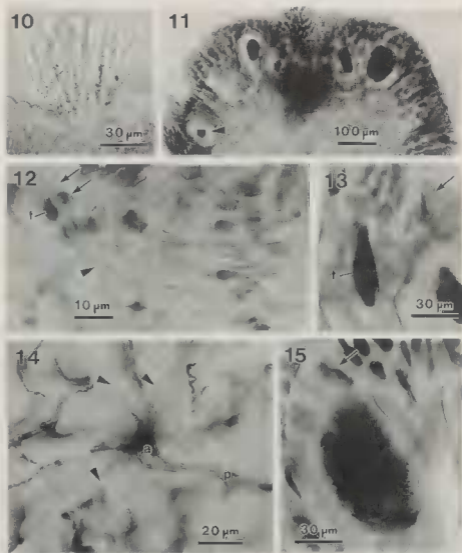
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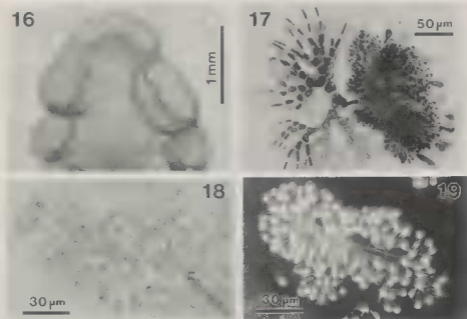
Figs 1-3. *Laurencia parvipapillata*. Formalin/seawater-preserved material. Fig. 1. Spermatangial specimen with four axes from a basal disc (arrowhead) collected at Kumejima Island (25.iii.1997). Fig. 2. Transverse section (TS) of the upper portion (near branched portion) of a first-order branch; arrowhead indicates the dorsal side (Kumejima Island, 25.iii.1997). Fig. 3A-C. TS of the upper portion of a first-order branch (at three different focal planes) showing each axial cell (a) connected with two periaxial cells (p) (stained with cotton blue; Pulau Manukan, 1.i.1996). a*, another axial cell shown in 3C.



Figs 4-9. *Laurencia parvipapillata*. Formalin/seawater-preserved material unless otherwise indicated. Fig. 4. Ventral surface near the apex of a first-order branch showing the absence of *corps en cerise* (living material; Kumejima Island, 25.iii.1997). Figs 5, 6. TS of the upper portion of a first-order branch: Fig. 5, the dorsal side; Fig. 6, the ventral side (Kumejima Island, 25.iii.1997). Fig. 7. Longitudinal section (LS) of the middle portion of a first-order branch showing a longitudinally oriented secondary pit-connection (arrowhead) between contiguous superficial cortical cells (stained with cotton blue; Pulau Manukan, 1.i.1996). Figs 8, 9. TS of the middle portion of a first-order branch showing a laterally oriented secondary pit-connection (arrowhead in Fig. 8) and a lateral fusion (arrowhead in Fig. 9) between contiguous superficial cortical cells (stained with cotton blue; Pulau Manukan, 1.i.1996).



Figs 10-15. *Laurencia parvipapillata*. Formalin/seawater-preserved material stained with cotton blue unless otherwise indicated (Kumejima Island, 25.iii.1997). Fig. 10. Trichoblast showing the cells without *corps en cerise* (living material). Fig. 11. LS of a tetrasporangial branch showing a perpendicular arrangement of the tetrasporangia; arrowhead indicates ■ abortive tetrasporangium. Fig. 12. Elongated fertile periaxial cell (arrowhead) producing a young tetrasporangium (t) and two cover cells (arrows) in LS. Fig. 13. More developed tetrasporangium (t) in LS; arrow indicates a cover cell (another being out of focus). Fig. 14. Axial cell (a) with a vegetative periaxial cell (p) and three fertile periaxial cells (arrowheads) in TS. Fig. 15. Mature tetrasporangium in LS; arrow indicates a cover cell (another being out of focus).



Figs 16-19. *Laurencia parvipapillata*. Formalin/seawater-preserved material (Kumejima Island, 25.iii.1997). Fig. 16. Fertile branchlets of a spermatangial plant. Fig. 17. Top view of a detached male trichoblast divided into a spermatangial branch and a sterile lateral at the suprabasal segment (stained with cotton blue). Fig. 18. Portion of a spermatangial branch (stained with cotton blue). Fig. 19. Epifluorescence microscopy of DAPI stained spermatangial branch; fluorescence indicating the position of each nucleus.